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Spore-dissemination of Equisetum.[1]

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(WITH PLATE IX.)

The subject of spore-dissemination of Equisetum may be considered under three heads:

I. Elongation of the axis of the spike.

II. Structure of the sporangium-wall and its mode of dehiscence.

III. Structure and action of the elaters.

Unless otherwise stated, these notes are wholly on Equisetum arvense preserved in alcohol.

I. *Elongation of the axis of the spike.*—In the immature spike the peltate scales which bear the sporangia on their inner surfaces are closely united edge to edge, forming an unbroken wall; but as the spores are nearing maturity the axis of the spike and the stalks of the peltate scales rapidly elongate, causing each scale to become separated by a considerable space from its neighbors. By careful comparison of cellular structure, this elongation seemed to be due to increase in length of cells. Longitudinal sections from the axis and scale-stalks of several spikes in which the scales were about to separate were made, and similar sections from the corresponding parts of spikes with separated scales. In each comparison the difference in length of cells was easily perceptible, the cells of the fundamental tissue in the different axes giving as the result of many measurements of length the ratio of 3 to 4. Thus, by the separation of the scales, resulting in the drying of sporangium-wall and spores, and furnishing a means of escape for the spores after they have left the sporangium, the first step in spore-dissemination is accomplished.

II. *Structure of the sporangium-wall and its mode of dehiscence.*—Each of the numerous scales of the spike is attached by a stalk running from the center of the scale to the main axis. Around the stalk and attached to the scale are from five to ten sporangia, arranged in a single row. A

[1]Contribution from the botanical laboratory of the University of Michigan.

sporangium is shaped like the finger of a glove. The dehiscence extends the whole length of the sporangium, and is always along the surface which is directed toward the stalk of the scale.

Examined with the microscope, the sporangium-wall is seen to be composed of several layers of cells. The attention is first caught by the appearance of the external layer of cells. These are found to have a definite arrangement, as indicated diagramatically in fig. 1. For convenience the surface of the sporangium which is nearest the stalk may be designated as the inner or ventral, and the opposite one as the outer or dorsal surface. Along the ventral surface are sometimes three, sometimes four, rows of cells, with their long axes at right angles to the long axis of the sporangium. Passing outward on each side from these rows of transverse cells the other cells of the external layer of the wall become more and more oblique, till on the dorsal surface they correspond in direction with the long axis of the sporangium.

In the three or four rows of transverse cells of the sporangium-wall, usually one row is of shorter cells than those composing the other rows, and the cells of this row are strengthened by rings. The transverse cells of the adjoining rows are marked by both rings and spirals; and the oblique and longitudinal cells are spiral, an annular cell being very rarely found among them (fig. 4). In Equisetum hyemale, however, though the transverse cells are mostly marked with rings, the other cells, without definite arrangement, are some annular and some spiral.

In addition to this outside layer of cells, the sporangium-wall contains two or three other layers of cells, not so conspicuous as the annular and spiral cells just described, but none the less constant. The sporangium-wall has been described by authors as composed of a single layer of cells. In Equisetum arvense and hyemale this is certainly not the case. These inner or lining cells have probably escaped notice because of the difficulty in detecting them by looking down upon or through the sporangium-wall. If sections of the sporangium be examined, the inner layers of cells become clearly visible. In working out this structure, groups of sporangia of Equisetum arvense were carefully imbedded in paraffin, and both longitudinal and transverse sections made on the rocking microtome. On examination, the tissue was found to have been injured in no way by the process of imbedding. Fig. 5 is a portion of a longitudinal section of a sporangium

with a part of the peltate scale and of the stalk: *a*, portion of the scale-stalk; *b*, section of the transverse cells of the ventral wall of the sporangium; *c*, section of the dorsal wall of the sporangium; below the sporangium is the scale in which the fibro-vascular bundle is seen to end. The spiral cells of the dorsal surface are continuous with the epidermal cells of the scale. Occasionally a spiral or annular celi is found in this epidermis. Fig. 6 is a transverse section of a sporangium-wall, midway between base and apex. In three positions—one dorsal and the other two lateral—the wall is strengthened not only by an increase in size of the spiral cells, but also by a greater number of the inner or lining cells. As we approach the region of the ventral transverse cells, the sporangium-wall becomes thinner and thinner by the decrease in number and size of the lining cells. Sometimes—as shown in fig. 6 at *a*—the lining cells can be seen to be continued across the external transverse cells; but here the inner cells are always reduced to a single very thin layer. Usually this layer of lining cells disappears in the ventral region; for it becomes closely appressed to the transverse cells. From the base to the apex of the sporangium, the lining cells are never more than one layer thick in the region of dehiscence, while dorsally and laterally these cells are three layers thick at the base and two layers thick at the apex.

Sablou[2] found that the length of the moist spiral cell was to that of the same cell when dry as 20 to 14, while the width is imperceptibly lessened.

In alcoholic material the relative length of the cell when moist and when dry is, with slight variation, as 2 to 1; the relative width, as 4 to 3. From the arrangement of the external cells of the wall, it is evident that the sporangium will contract in length much more along the dorsal than along the ventral surface. In fig. 3 the position of the line of dehiscence in the moist sporangium is indicated by an unbroken line. From what we know concerning the arrangement of the external cells and their contraction, we should expect, in drying, one edge of the wall along the line of dehiscence to move to the position indicated in fig. 3 by a dotted line—this line moving, as it passes from the base, more and more from its original position. And this is exactly what happens, as shown by fig. 2, which gives the appearance of an open sporangium.

[2]Annales des Science, 7 Series, Tome 2.

The act of dehiscence of the sporangium was observed in six cases. The rupture begins near the apex, a little toward the ventral surface. The opening is at first irregular, with radiating lines extending between surrounding cells; but soon the dehiscence takes a definite direction between two rows of transverse cells—this being the place where the wall is thinnest, and the line between adjacent rows of external cells straightest. The line of dehiscence in its descent to the base frequently passes from one side of a row of transverse cells to the other side. Near the apex especially the dehiscence is usually quite irregular, as shown in fig. 2.

What is the function of the transverse cells? It can not be merely to pull the wall apart; this is accomplished in a greater degree by the oblique and longitudinal cells. The transverse cells prevent the ventral wall of the sporangium from shortening equally with the dorsal wall—thus assisting in dehiscence and causing the edges of the open sporangium to gape widely.

III. *Structure and action of the elaters.*—The external coat of the spore divides at maturity into four narrow, spiral bands—the so-called elaters—as shown in fig. 7. If the spore be allowed to dry, or if it be immersed in glycerine, the elaters will unwind as shown in fig. 8, remaining attached to the spore at one point. If in fig. 7 we call the positions of the expanded ends of the elaters the poles of the spore, then the elaters are attached to the spore at the equator. When the elaters are outstretched they may, as stated by Sachs, assume the form of a cross; but they do not cross one another. Often, in straightening out, the elaters become detached from the spore. If one such detached elater be examined, there will frequently be found, about half-way from end to end, a very thin bit of membrane attached by one edge to the elater (fig. 8). This piece of membrane has the appearance of having been peeled off the surface of the spore.

To account for the hygroscopic movements of the spores, the elaters have been described by Sablou as composed of two layers—an external cellulose layer, and an internal layer of lignine. Two layers may be demonstrated both mechanically and chemically. If pressure be exerted on the cover-glass so as to crush the spores underneath, some of the elaters will be found in the condition shown in fig. 10. Here there is an evident separation between the two layers. If spores be placed in Schultze's solution or in picrocarmine,

the two layers of the elater are differently stained. The outer layer is probably cellulose and the inner lignine, as stated by Sablou. In Schultze's solution the outer layer does not seem to give a characteristic cellulose reaction; the inner layer is stained yellowish brown. In iodine solution, with subsequent addition of sulphuric acid, the outer layer of the elater shows, after an hour or two, a decidedly blue color.

Perhaps the most noticeable feature of the minute structure of the elaters is the striation of the cellulose layer, distinguishable without the use of reagents, but made a little more distinct by the application of caustic potash. Everything seems to indicate that the cellulose layer is built up of oblique laminæ, separated by much thinner plates of a substance of different refractive power. If an elater lies in a position vertical to the view, with either its external or lateral surface toward the observer, the direction of the laminæ is from left to right downward (figs. 10–11). That these are really laminæ is proved by their tendency to separate under pressure instead of breaking across (fig. 11). By actual measurement, these laminæ are found to be thinner when dry than when moist. The result of such shrinking is the unwinding of the elaters, provided that the shrinkage is less in the inner layer. A cross-section of an elater gives the form indicated in fig. 12.

RECAPITULATION: I. The first step in spore-dissemination is the separation of the sporangia-bearing scales by the elongation of the axis of the spike, thus allowing free circulation of air for drying spores and sporangia, and providing open spaces for the escape of the spores after dehiscence of the dry sporangia.

II. The comparatively straight columns or rows of transverse cells in the ventral wall of the sporangium, together with the thinning out of the wall in this region, furnishes a line of weakness which becomes the line of dehiscence. Moreover, the unequal contraction in length and width of the strong external layer of cells of the sporangium-wall results in a great shortening of the dorsal wall and a slight shortening of the ventral wall, thus causing a wide opening in the ruptured sporangium for the passage of the spores.

The hygroscopic properties of the elaters seem to be satisfactorily explained by the difference in chemical composition of the two layers composing them.

The function of the elaters is twofold: (1) to push the

spores out of the sporangia; (2) to furnish sails for catching the wind by which the spores are distributed.

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EXPLANATION OF PLATE IX.—Fig. 1. Sporangium of Equisetum arvense, × 80. This figure is diagrammatic; but the cells are represented in true position and size; *a*, probable line of dehiscence; on each side of this line are the transverse cells; at the left are the longitudinal cells of the dorsal wall; and between transverse and longitudinal cells are the oblique cells.

Fig. 2. Sporangium of E. arvense after dehiscence, × 30.

Fig. 3. Diagram of a sporangium of E. arvense, × 30. The unbroken median line shows the position of the line of dehiscence before rupture; the dotted line shows the relative amount of shortening of the dorsal and ventral surfaces of the dry sporangium. The dotted line would also represent one border of the gape into the ruptured sporangium.

Fig. 4. Portion of the wall of E. arvense, to show cells in the region of the line of dehiscence, × 175. Here are three rows of transverse cells containing rings and spirals.

Fig. 5. Longitudinal section of the lower part of a sporangium of E. arvense, with a portion of the scale and scale stalk, × 125: *a*, cells of the scale stalk; *b*, section of the ventral transverse cells of the sporangium-wall; *c*, section of the dorsal wall of the sporangium. Below the cavity of the sporangium is a portion of the peltate scale.

Fig. 6. Transverse section of a sporangium of E. arvense, midway between base and apex, × 125: *a*, probable location of the line of dehiscence.

Fig. 7. Spore of E. arvense, with the elaters beginning to unwind, × 350.

Fig. 8. Same with elaters outstretched, × 350.

Fig. 9. One of the elaters of the same, showing triangular membrane at the place of attachment, × 350.

Fig. 10. Portion of an elater of the same, showing separation of cellulose from the inner layer, × 700.

Fig. 11. Expanded end of an elater of E. arvense, showing a split between the laminæ, × 700.

Fig. 12. Cross-section of an elater of the same, × 700.

Personal reminiscences of Dr. Asa Gray.[1]

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The greatest of America's botanists, Asa Gray, will nevertheless be remembered for many other qualities. He was essentially a self-made man, and rose to prëeminence through his own good qualities of heart and head, coupled with enthusiasm and perseverance. There was nothing stilted or

[1]Remarks made at the Gray memorial meeting, held by the Biological Society of Washington, April 5, 1888.